

Article



http://dx.doi.org/10.11646/zootaxa.4032.5.4 http://zoobank.org/urn:lsid:zoobank.org:pub:AB088190-F950-4EDA-BA91-AB180D2B705D

Silversides of the genus Labidesthes (Atheriniformes: Atherinopsidae)

DAVID C. WERNEKE¹ & JONATHAN W. ARMBRUSTER²

101 Rouse Life Sciences, Department of Biological Sciences, Auburn University, AL 36849. E-mail: \(^1\)wernedc@auburn.edu; \(^2\)armbrjw@auburn.edu

Abstract

The two species of *Labidesthes, L. sicculus* and *L. vanhyningi*, are herein redescribed. *Labidesthes sicculus* is separated from *L. vanhyningi* by the presence of an anterolateral process of the post temporal that is longer than it is wide (versus wider than long), a ratio of thoracic length to abdominal length greater than two (versus less than two), and a midlateral stripe that is narrows in front of first dorsal fin (versus expanding in front of first dorsal fin). *Labidesthes sicculus* is found in Gulf of Mexico drainages from the Brazos River East to the Pascagoula River, Mississippi River (absent in middle and upper Missouri River), and Great Lakes-St. Lawrence River (absent in Lake Superior). *Labidesthes vanhyningi* is found in Gulf Mexico drainages from the Neches River East around peninsular Florida North on the Atlantic Coast to the Pee Dee River, in the Mississippi River it is confined to lowland areas of the Lower Mississippi River.

Key words: Silverside, Menidiini, Menidiinae, North America

Introduction

Labidesthes sicculus, the brook silverside, is the most widespread freshwater atherinopsid in North America, occurring natively in drainages on the Atlantic slope from the Santee River south to the Everglades, Gulf of Mexico drainages west to Galveston Bay, and the Great Lakes-St. Lawrence River drainage (Fig. 1) (Etnier & Starnes 1993; Page & Burr 2011). Habitat alteration and introductions over the last century have increased the range of L. sicculus beyond its native distribution (Lee 1978; Rowe 1992; Marsden et al. 2000). Two species have been described within Labidesthes, L. sicculus (Cope) and L. vanhyningi Bean and Reid; however, only L. sicculus is currently considered valid.

Labidesthes is a member of the tribe Menidiini within the subfamily Menidiinae of the Atherinopsidae (Chernoff 1986; Dyer & Chernoff 1996). The brook silverside was originally described by Cope (1865) as Chirostoma sicculum from specimens collected in the Detroit River, Michigan. Citing differences with Chirostoma such as a "duck-like muzzle" (Cope 1870:455) and premaxillaries separated by a medial groove, Cope described the genus Labidesthes for the brook silverside. A second species, L. vanhyningi, was described by Bean & Reid (1930) from Prairie Creek outside Gainesville, Florida. Bean & Reid (1930), separated L. vanhyningi from L. sicculus by stating that it was more slender, less compressed, and had a shorter snout, among other characters. In their description of L. vanhyningi, Bean & Reid (1930) only included specimens from Alachua County, Florida, and they did not define a range for the new species. Hubbs & Allen (1943, p. 128) considered L. vanhyningi a subspecies of L. sicculus, noting that it "is a rather poorly defined geographical subspecies." Hubbs & Lagler (1947) state that Labidesthes in the southeast were L. s. vanhyningi, and further noted that southwestern populations might represent a third distinct form. Bailey et al. (1954) placed L. vanhyningi in the synonomy of L. sicculus when they found putatively diagnostic characters sensu Bean & Reid (1930) of L. vanhyningi in populations of Labidesthes from Arkansas, and they recommended further investigation before L. vanhyningi be reelevated. Rasmussen (1980) summarized developmental differences between his findings and those of other works, and noted that the differences in myomere counts and attachment filaments were clinal, but he cited the need for additional work on different populations to resolve the taxonomy of *Labidesthes*.

While evidence supporting a morphological separation of Labidesthes is currently lacking, literature regarding

life history and reproductive mechanisms indicates that there are at least two separate species under the biological species concept (Mayr 1942). Spawning accounts of northern United States populations in Michighan and Wisconsin indicated that *L. sicculus* were releasing eggs upon spawning (Hubbs 1921; Cahn 1927). Powells & Sandeman (2008) also concluded that eggs were released during mating, and found no evidence of sperm or embryos in female *Labidesthes* from Ontario, Canada. Grier *et al.* (1990) found eyed embryos inside of females collected from southern *Labidesthes* in Florida proving that fertilization, at least in that population, was internal.

Only one phylogenetic study has included species of *Labidesthes* from across their range. Bloom *et al.* (2009) found 14.7% sequence divergence between specimens from Florida and Minnesota in the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene. Although these populations are from almost opposite ends of the range of *Labidesthes*, the results suggest that there is a taxonomic difference between populations.

This study examines morphometric, meristic, and osteological data among populations of *Labidesthes* across their range to determine the taxonomic status of *L. vanhyningi*. The species of *Labidesthes* are herein redescribed, the ranges of the species are defined, and aspects of *Labidesthes* distribution are discussed.

Methods

Institutional abbreviations follow Sabaj Pérez (2014). Numbers of specimens used in analyses are in parentheses in material examined. Specimens from localities not available through museums were collected using seine nets. Fish were anesthetized in MS-222 upon capture, and preserved in a solution of 10% formalin in water for one week. Preserved specimens were soaked in water for three days to remove formalin from the tissues. Fish were then placed in 70% ethanol, and accessioned at AUM. Clearing and staining procedures followed Taylor & Van Dyke (1985). Sixty-four specimens were used in the skeletal analysis and are indicated by "c&s" in Materials Examined. Meristics follow Hubbs & Lagler (1964) with the following exceptions: median lateral scale rows follow Barbour (1973), interdorsal scales are the scales between the first and second dorsal fins, postdorsal scales are the scales between the second dorsal fin and the first dorsal procurrent caudal-fin ray, anus-anal-fin scales are the scales between the anus and the anal fin, and postanal scales are the scales between the anal fin and the first ventral procurrent caudal-fin ray. A Principal Components Analysis (PCA) was performed using a covariance matrix in JMP Pro ver. 11 (SAS Institute Inc 2013). To determine statistical significance, specimens were separated into two groups based on differences observed in osteology and pigmentation. Meristics in parentheses represent values outside the 95% confidence interval.

TABLE 1. Definitions of geometric morphometric landmarks.

Landmark	Definition			
1	Tip of Snout			
2	Upper labial fold			
3	Tip of posterior process of supraoccipital			
4	Anterior insertion of first dorsal fin			
5	Posterior insertion of first dorsal fin			
6	Anterior insertion of second dorsal fin			
7	Posterior insertion of second dorsal fin			
8	Insertion of dorsal procurrent caudal-fin rays			
9	Insertion of ventral procurrent caudal-fin rays			
10	Posterior insertion of anal fin			
11	Anterior insertion of anal fin			
12	Vent			
13	Anterior insertion of pelvic fin			
14	Symphysis of coracoids			
15	Anterior margin of orbit			
16	Posterior margin of orbit			

Geometric morphometric data (Rohlf and Marcus 1993; Adams *et al.* 2004) were collected by digitally photographing specimens used in the meristic analysis with a Nikon Coolpix 990 digital. Images were coalesced into a tps file using tpsUtil 1.58 (Rohlf 2013) and 17 landmarks (Fig. 2; Table 1) were digitized in tpsDig 2.17 (Rohlf 2013). TpsUtil was used to convert the tps file to an NTSPC file that was analyzed in MorphoJ (Klingenberg 2011). A Generalized Procrustes Analysis was used to align landmarks (Rohlf and Slice 1990; Klingenberg and Spence 1993; Boulesteix 2005; Mitteroecker and Bookstein 2011). A covariance matrix was constructed, and a Canonical Variate Analysis (CVA) and a (PCA) were performed (Rohlf *et al.* 1996). Permutation tests for Mahalanobis pairwise distances were performed with 10,000 replictations in the CVA to determine if groups were significantly different from each other (Klingenberg and Monteiro, 2005).

Measurements were made with digital calipers to the nearest 0.01 mm. In addition to standard length, two measurements of pelvic fin placement were made as follows: thoracic length is the distance from the symphysis of the coracoids to the anterior insertion of the pelvic fin, abdominal length is the distance from the anterior insertion of the pelvic fin to the urogenital opening. To determine intrapopulational variation, drainages with low numbers of individuals were combined with adjacent drainages to reduce error attributable to small sample sizes. Species distributions were extrapolated by examining an additional 8,516 specimens for external diagnostic characters following the initial analysis. Geographic coordinates for all material examined were plotted in Magic Maps (ver. 1.4.9) using map layers from Natural Earth (naturalearthdata.com).

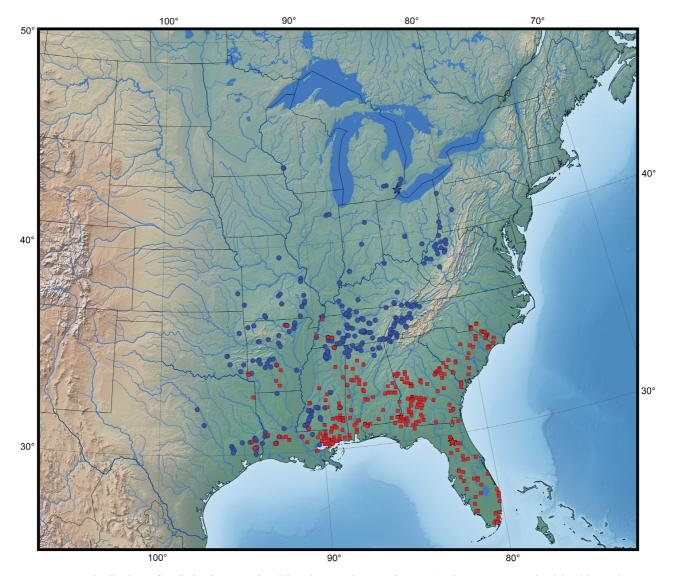


FIGURE 1. Distribution of *Labidesthes sicculus* (blue dots) and *L. vanhyningi* (red squares) examined in this study. Stars indicate type localities.

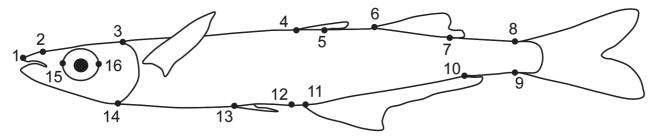


FIGURE 2. Location of landmarks used in geometric morphometric analysis.

Labidesthes Cope 1870

Labidesthes sicculus (Cope 1865)

Brook Silverside (Figs. 3–4)

Chirostoma sicculum Cope, 1865. Proc. Acad. Nat. Sci. Phila. 17:81.

Material examined. Syntypes: UMMZ 213812, (2), 52–53 mm SL, Grosse Isle, Detroit River, Wayne County, Michigan, by M. Miles.

Nontypes: Arkansas River drainage: NCSM 4544, NCSM 47064, NCSM 47499, TU 12004, UAIC 1013.05 (2), UF 21983 (1), UF 22016 (2), UT 158.43, UT 158.252.

Brazos River drainage: NCSM 36393, TU 91175.

Calcasieu River drainage: TU 44611, TU 64284, TU 121912, TU 124813.

Cumberland River drainage: AUM 28924 (7), NCSM 29291, NCSM 48033, NCSM 48342, UAIC 12354.01 (2 + 2 c&s), UT 158.13, UT 158.26, UT 158.40, UT 158.42, UT 158.105, UT 158.108, UT 158.110, UT 158.111, UT 158.117, UT 158.134, UT 158.139, UT 158.238, UT 158.273, UT 158.274, UT 158.281, UT 158.285, UT 158.324, UT 158.379.

Galveston Bay drainage: TU 61893, TU 61963, TU 62852, TU 66483, TU 67260, UF 29642 (3), UF 29466 (2 c&s).

Great Lakes & St. Lawrence River drainage: TU 19209, UAIC 2985.11 (2), UMMZ 117154 (5 + 2 c&s), UMMZ 132001 (5).

Homochitto River drainage: AUM 50798, AUM 50799, AUM 50803, AUM 50814, AUM 50822, INHS 90112 (2), TU 7439, TU 46524, TU 76761, TU 83817.

Illinois River drainage: AUM 29752 (1), NCSM 47475, UT 158.79.

Meramec River drainage: NCSM 30651, UT 158.109.

Lower Mississippi River drainage: AUM 19060 (1), INHS 76651 (5), NCSM 33682, NCSM 47089, TU 75572, TU 91073, TU 91155, TU 91191, UAIC 6401.07 (1 + 1 c&s), UT 158.83, UT 158.86, UT 158.88, UT 158.118, UT 158.204, UT 158.215, UT 158.216, UT 158.221, UT 158.224, UT 158.233, UT 158.235.

Upper Mississippi River drainage: NCSM 36800, UT 158.261, UT 158.262, UT 158.263.

Missouri River drainage: NCSM 30641, UT 158.179, UT 158.199, UT 158.378.

Neches River drainage: TU 21701, TU 67309, TU 72745, TU 109553, TU 110175, TU 111132, TU 111685, TU 114868, TU 122991.

Ohio River drainage: INHS 42358 (5 + 2 c&s), INHS 43459 (5), NCSM 37765, NCSM 38285, NCSM 38432, NCSM 38652, NCSM 38738, NCSM 38837, NCSM 38853, NCSM 38880, NCSM 39165, NCSM 39376, NCSM 55230, NCSM 55231, NCSM 55232, NCSM 55233, NCSM 55234, NCSM 55235, NCSM 55236, NCSM 55245, NCSM 55246, UAIC 2844.14 (1), UT 158.69, UT 158.70, UT 158.71, UT 158.72, UT 158.73, UT 158.228, UT 158.268.

Pascagoula River drainage: UT 158.291, UT 158.292.

Pearl River drainage: TU 191982, TU 28962, TU 28996, TU 82034, UT 158.87, UT 158.286, UT 158.289, UT 158.290, UAIC 12767.11 (2 + 2 c&s), UAIC 12770.07 (1).



FIGURE 3. *Labidesthes sicculus* preserved specimen dorsal, lateral, and ventral views. AUM 62249, 71.1 mm SL, Tennessee River drainage, Maury County, TN.

Lake Pontchartrain drainage: TU 45320, TU 76058.

Red River drainage: AUM 13762 (2 c&s), AUM 34112 (5), INHS 44515 (5), NCSM 4493, NCSM 36288, NCSM 36329, NCSM 37363, NCSM 37390, NCSM 37424, NCSM 37482, NCSM 47153, TU 147500, TU 192087, UT 158.23, UT 158.266.

Sabine River drainage: TU 61519, TU 62377, TU 67587, TU 67765, UF 29501 (1).

Tennessee River drainage: AUM 12012 (2 c&s), AUM 29655 (5), NCSM 26857, NCSM 29338, NCSM 29624, UAIC 13312.23 (5), UT 158.2, UT 158.9, UT 158.25, UT 158.29, UT 158.44, UT 158.65, UT 158.66, UT 158.91, UT 158.96, UT 158.97, UT 158.98, UT 158.100, UT 158.104, UT 158.113, UT 158.123, UT 158.126, UT 158.127, UT 158.129, UT 158.137, UT 158.138, UT 158.140, UT 158.160, UT 158.162, UT 158.163, UT 158.171, UT 158.172, UT 158.173, UT 158.180, UT 158.181, UT 158.182, UT 158.183, UT 158.184, UT 158.186, UT 158.187, UT 158.200, UT 158.201, UT 158.203, UT 158.208, UT 158.209, UT 158.212, UT 158.213, UT 158.214, UT 158.217, UT 158.218, UT 158.227, UT 158.236, UT 158.237, UT 158.241, UT 158.242, UT 158.259, UT 158.267, UT 158.277, UT 158.280, UT 158.294, UT 158.395, UT 158.305, UT 158.309, UT 158.311, UT 158.312, UT 158.313, UT 158.314, UT 158.315, UT 158.316, UT 158.317, UT 158.318, UT 158.319, UT 158.320, UT 158.321, UT 158.321, UT 158.322, UT 158.323, UT 158.326, UT 158.326, UT 158.327.

White River drainage: AUM 33957 (5), INHS 81779 (5), NCSM 37452, NCSM 37502, NCSM 37528, NCSM 47128, NCSM 47369, UT 158.30, UT 158.31, UT 158.101, UT 158.112, UT 158.264, UT 158.265, UT 158.377.

Yazoo River drainage: AUM 30226 (2 c&s), AUM 50801, AUM 50802, AUM 50805, AUM 50811, AUM 50813, AUM 50815, AUM 50816, AUM 50817, AUM 50820, AUM 50821, AUM 50826, AUM 50828, AUM 50830, AUM 50831.

Diagnosis. Labidesthes sicculus differs from Labidesthes vanhyningi in having the anterolateral process of the post-temporal longer than width of base (vs. shorter than the base: Fig. 5), a midlateral stripe that tapers anterior of the first dorsal fin to a point behind the dorsal insertion of the pectoral fin (vs. maintaining width or expanding anterior of first dorsal fin:Fig. 3), and a ratio of thoracic length to abdominal length greater than 2 (vs. less than 2).

Description. Meristics: median lateral scale rows (69–71) 72–91 (92); scales above midline 8–10 (11); scales below midline 8–11; peduncle scales 18–22; predorsal scales 36–48 (49); interdorsal scales (9) 10–15; prepelvic scales (22–23) 24–32; anus-anal-fin scales 3–6 (7); postdorsal scales 14–20; postanal scales 10–16; first dorsal III–V (6); second dorsal I,8–12; pectoral 11–13; pelvic 6; anal-fin I,(19) 20–26 (27); caudal 16–17 (Table 2).

TABLE 2. Mode and range of *Labidesthes* meristics.

	L. sicculus		L. vanhyningi	
Meristics	Mode	Range	Mode	Range
1st dorsal spines	4	3–6	5	3–6
2nd dorsal spines	1	1–1	1	1–1
2nd dorsal rays	10	8–12	10	8–12
Pectoral rays	12	11–13	12	11–14
Pelvic rays	6	6–6	6	6–6
Anal spines	1	1–1	1	1–1
Anal rays	23	19–27	22	18–26
Principal Caudal Rays	17	16–17	17	15–18
Midlateral scales	78	69–92	77	65–91
Scales above midline	9	8–11	9	8–11
Sacles below midline	9	8–11	9	7–11
Circumpeduncle scales	20	18–22	20	16–22
Predorsal scales	39	35–49	36	31–46
Interdorsal scales	12	9–15	12	9–17
Prepelvic scales	27	20–32	23	20–30
Anus-anal fin scales	4	3–7	3	2–6
Post dorsal scales	17	14–21	17	12–22
Post anal scales	13	10–16	10	8–14

Morphometrics: specimens examined 52.7–82.5 mm; short head, four times into SL; eye large, 2.5 times into maximum body depth. Body compressed and elongate, maximum body depth six to eight times into SL, ratio of thoracic length to abdominal length greater than two.

Premaxillary long, weakly protrusible, curving ventrally midway along length, creating muzzle like snout; terminal mouth, with moderately long, posteriorly curved, pointed, conical teeth. Forked caudal fin; second dorsal and anal fins falcate; anal fin long, extending length from anterior of first dorsal to beyond posterior of second dorsal; pelvic fin extending to anus; first dorsal-fin origin opposite of anal-fin origin; pectoral fin pointed, extending to insertion of pelvic fin. First dorsal spinous, second dorsal with one anterior spine followed by branched rays. Genital papilla short in males, absent in females. Lateral line nearly absent, pored scales, if present, always found posterior to first dorsal usually concentrated on peduncle. Scales cycloid, extending onto caudal fin, absent from other fins; opercle scaled, scales extending to a spot below front of eye; top of head with or without scales, if present may extend to front of eye. Dorsal profile ascending gradually from tip of snout to supraoccipital, profile from supraoccipital to anterior insertion of second dorsal straight, and descending gradually to dorsal procurrent caudal-fin rays. Ventral profile forming gentle arc from snout to ventral procurrent caudal-fin rays.



FIGURE 4. Syntypes of *Chirostoma sicculum*, UMMZ 213812 (A. 53 mm SL, B. 52 mm SL) and C. holotype of *Labidesthes vanhyningi* USNM 88485 58 mm SL. Scale bars equal 1 cm (shared for A and B). A and B by Ann Barget and the Great Lakes Invasive Species (UMMZ) project and C by Sandra J. Raredon, Smithsonian Institution, National Museum of Natural History.

Color in life. Body translucent, often with yellow or green tint. Midlateral silver band, narrowest on caudal peduncle, broadening and fading anteriorly. Scales above midline and on dorsum outlined with melanophores, forming weak band along center of dorsum. Venter with black stripe originating posterior to anus and terminating at the origin of caudal fin. Distal one-third of first dorsal fin with melanophores on membranes forming a black band in males, not as pronounced in females. Head covered in melanophores, with supraoccipital densely pigmented, chin pigmented, dark spot on lower jaw at rear margin of mouth. Iris silver, dusky dorsally in some individuals, inside of mouth with scattered melanophores along margin and on outside of cheeks. Spines and rays outlined in melanophores, except pelvic fin, which is devoid of pigment. Silver peritoneum visible through body wall.

Color in alcohol. Body pallid, lateral silver stripe along the midline overlaying a dark stripe, fading anteriorly, dark stripe narrowing in advance of first dorsal fin as it approaches pectoral fin. (Fig. 3). Scales above lateral stripe outlined in melanophores, dorsum with black stripe along middle. Scales below lateral stripe faintly pigmented in some individuals. Venter with black stripe originating posterior to anus and terminating at origin of caudal fin. Distal one-third of first dorsal fin with melanophores on membranes forming black band in males, but not as pronounced in females. Head covered in melanophores, with occiput densely pigmented, chin darkly pigmented, dark spot on lower jaw at rear margin of mouth. Iris silver, dusky dorsally in some individuals, inside of mouth with scattered melanophores along margin and on outside of cheeks. Spines and rays outlined in melanophores, except in pelvic fin, which is devoid of pigment.

Range. Labidesthes sicculus occurs in Gulf of Mexico drainages from the Pearl River west to Brazos River (including the Mississippi River drainage), and the Great Lakes (excluding Lake Superior)-St. Lawrence River drainages (Fig. 1).

Etymology. Likely, from the latin *sicula* meaning small dagger (Scharpf & Lazara 2014).

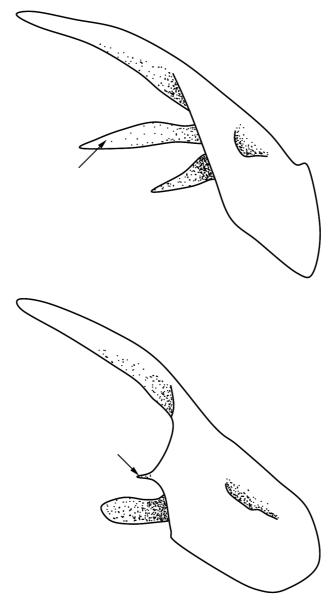


FIGURE 5. The anterolateral process of the post temporal (indicated by arrows) is longer than its width in *Labidesthes sicculus* (A.) and shorter than its width in *L. vanhyningi* (B.).

Labidesthes vanhyningi Bean and Reid 1930

Golden Silverside (Figs. 4, 6–7)

Labidesthes vanhyningi Bean and Reid, 1930. Proc. Biol. Soc. Wash. 43:193-194.

Material examined. *Holotype:* USNM 88485 (1), 58 mm SL, 20 January 1927, Prairie Creek, six miles east of Gainesville, Florida, by O.C. Van Hyning.

Nontypes: Altamaha River drainage: AUM 27529 (2 + 2 c&s), UT 158.36, UT 158.188, UT 158.189, UT 158.190, UT 158.260, UT 158.275, UT 158.284, UT 158.380.

Apalachicola River drainage: AUM 11557 (3), AUM 14268 (2), AUM 29164 (1), AUM 29625 (2 + 2 c&s), AUM 30021 (1), AUM 30977 (1), AUM 31040 (1), AUM 32041 (2), AUM 34350 (6), AUM 37383 (2), NCSM 28067, NCSM 28101, NCSM 28127, UAIC 1675.09 (2), UAIC 7774.05 (7), UAIC 9713.06 (2), UF 105469 (3), UT 158.143, UT 158.145, UT 158.149, UT 158.150, UT 158.151, UT 158.152, UT 158.153, UT 158.155, UT 158.156, UT 158.157, UT 158.169, UT 158.170, UT 158.174, UT 158.175, UT 158.177, UT 158.178, UT 158.197, UT

158.198, UT 158.219, UT 158.222, UT 158.226, UT 158.230, UT 158.231, UT 158.232, UT 158.234, UT 158.243, UT 158.244, UT 158.245, UT 158.246, UT 158.247, UT 158.248, UT 158.249, UT 158.250, UT 158.251, UT 158.257, UT 158.258, UT 158.269, UT 158.278, UT 158.381.

Atchafalaya River drainage: TU 959, TU 87382.

Biloxi Bay drainage: AUM 50823, TU 137964, TU 142348, TU 143040. Calcasieu River drainage: TU 41495, TU 123267, TU 200886, TU 203234.

Caloosahatchee River drainage: NCSM 27388. Cape Fear River drainage: NCSM 60434.

Choctawhatchee River drainage: AUM 31534, NCSM 55223.

Edisto River drainage: NCSM 25757, NCSM 25792, NCSM 25821, NCSM 25848, NCSM 25927.

Escambia River drainage: AUM 21393 (2), INHS 38424 (5), UAIC 11025.10 (1), UAIC 11645.07 (1), UT 158.81.

Everglades drainage: NCSM 27375, NCSM 27411, NCSM 27421, NCSM 27434, NCSM 27472, NCSM 27545, NCSM 27851, NCSM 29032, NCSM 29652, NCSM 29673, UF 17 (1), UF 6901 (3), UF 34425 (1), UF 34742 (1), UF 35071 (1), UF 44096 (3), UF 101937 (1), UF 102735 (1), UF 112022 (1), UF 127966 (2), UF 127967 (4).

Florida Atlantic Coast drainages: AUM 11369 (1), AUM 15042 (1), AUM 21204 (4 + 2 c&s), AUM 34037 (4), NCSM 28153, NCSM 31853, NCSM 55243, NCSM 55244, TU 12411, UF 26353 (3), UF 84245 (1), UF 127963 (4 + 2 c&s), UF 127964 (4), UF 127965 (2), UT 158.47.

Hillsborough Bay drainage: AUM 31984 (5 + 2 c&s), UAIC 8935.09 (2), UF 90879 (5).

Mermentau River drainage: TU 44562.

Lower Mississippi River drainage: TU 44891, TU 71386, TU 140587, UAIC 10297.12 (2), UT 158.90, UT 158.21, UT 158.125, UT 158.220, UT 158.390, UT 158.391, UT 158.393.

Mobile Bay drainage: AUM 6550 (7), AUM 7835 (1), AUM 8871 (1), AUM 13234 (1), AUM 19508 (1), AUM 19730 (1), AUM 21969 (2), AUM 22987 (1), AUM 30853 (2 c&s), AUM 30893 (3 + 2 c&s), AUM 31257 (1), AUM 32386 (1), AUM 33385 (1), AUM 34547 (2 c&s), AUM 50818, AUM 50832, NCSM 55238, UAIC 340.05 (1), UAIC 1087.13 (2 c&s), UAIC 1325.04 (3), UAIC 2013.09 (2), UAIC 3836.12 (1), UAIC 4079.15 (6 + 2 c&s), UAIC 4537.14 (1), UAIC 4579.09 (5), UAIC 6112.14 (3), UAIC 6120.08 (2), UAIC 6779.10 (1 + 2 c&s), UAIC 7024.09 (1), UAIC 7047.10 (1), UAIC 7195.12 (1), UAIC 9922.01 (2), UAIC 9924.01 (4), UAIC 10545.06 (3), UAIC 11292.01 (1), UAIC 11295.15 (1), UAIC 11704.07 (2), UAIC 12545.03 (1), UT 158.16, UT 158.205, UT 158.206, UT 158.207, UT 158.82.

Ochlockonee River drainage: AUM 26510 (1), UF 54415 (4), UT 158.144, UT 158.146, UT 158.158, UT 158.211, UT 158.229.

Ogeechee River drainage: AUM 33363 (2), UT 158.191, UT 158.193, UT 158.194, UT 158.195.

Pascagoula River drainage: AUM50796, AUM 50797, AUM 50800, AUM 50804, AUM 50807, AUM 50808, AUM 50809, AUM 50810, AUM 50812, AUM 50819, AUM 50824, AUM 50825, AUM 50827, AUM 50829, NCSM 55239, NCSM 55240, NCSM 55241, NCSM 55242, TU 52078, TU 54736, TU 57457, TU 57479, TU 60476, TU 89722, TU 100014, TU 100070, UT 158.86, UT 158.392, UT 158.394.

Peace River drainage: AUM 14706 (4 + 1 c&s), NCSM 27498, UF 79631 (4), UT 158.32.

Pearl River drainage: AUM 14558 (1), AUM 50806, TU 7674, TU 7692, TU 7934, TU 14112, TU 25796, TU 39714, TU 43493, TU 45837, TU 45907, TU 68758, TU 81759, TU 188570.

Pee Dee River drainage: AUM 35256 (1), NCSM 21991, NCSM 22000, NCSM 25695, NCSM 25744, NCSM 25862, NCSM 25985, NCSM 26864, NCSM 26869, NCSM 26874, NCSM 28374, NCSM 28619, NCSM 28903, NCSM 29651, NCSM 30115, NCSM 30120, NCSM 30135, NCSM 30850, NCSM 30867, NCSM 31002, NCSM 31106, NCSM 31135, NCSM 31407, NCSM 31649, NCSM 33205, NCSM 33285, NCSM 35005, NCSM 35879, NCSM 35884, NCSM 35888, NCSM 35893, NCSM 35894, NCSM 45232, NCSM 46972, NCSM 51787, UT 158.310.

Lake Pontchartrain drainage: NCSM 55237, TU 1376, TU 238, TU 46114, TU 74932, TU 106950, TU 109877, TU 116482, TU 116685, TU 119388, TU 200887.

Neches River drainage: TU 106407, TU 200888, TU 200889.

Red River drainage: NCSM 36316, NCSM 36612, NCSM 37403, NCSM 37403, NCSM 37416, NCSM 55222, UAIC 778.02 (1), UT 158.22, UT 158.41.

Sabine River drainage: AUM 26380 (1), TU 114924, UF 29501 (1).

St. Helena Sound drainage: UT 158.24.

Bay St. Louis drainage: TU 4515, TU 7658, TU 8006, TU 14824, TU 64633, TU 68424, TU 79818, TU 89124, TU 133002, TU 134463, TU 153859, UAIC 1733.04 (2).

Santee River drainage: AUM 20393 (2 + 2 c&s), NCSM 46673.

Satilla River drainage: AUM 5012 (4), AUM 11278 (2 c&s), AUM 23041 (3), UF 23728 (1).

Savannah River drainage: AUM 24303 (1), AUM 24371 (2 + 2 c&s), AUM 24403 (1), NCSM 16790, NCSM 22905, NCSM 24780, NCSM 25094, UT 158.164, UT 158.165, UT 158.176, UT 158.276, UT 158.287, UT 158.288.

Suwannee River drainage: AUM 8969 (2), AUM 8993 (1), AUM 10263 (2), AUM 22079 (2 c&s), AUM 31977 (5), UMMZ 136575 (5 + 2 c&s), UT 158.14, UT 158.154, UT 158.159.

Withlacoochee River drainage: UF 120301 (10).

Yellow River drainage: AUM 31474 (2).

Diagnosis. Labidesthes vanhyningi differs from L. sicculus in having the anterolateral processes of the post-temporals shorter than width of the base (vs. longer than width of base: Fig. 5), a midlateral stripe that does not taper, usually expanding, to insertion of pectoral fin in advance of the first dorsal-fin (vs. tapering to insertion of pectoral fin in advance of first dorsal fin: Figs. 6 & 7), and a ratio of thoracic length to abdominal length less than 2 (vs. greater than 2).



FIGURE 6. Labidesthes vanhyningi preserved specimen dorsal, lateral, and ventral views. AUM 21204, 62.95 mm SL, St. John's River drainage, Marion County, FL.

Description. Meristics: median lateral scale rows (65–67) 68–88 (89–91); scales above midline 8–11; scales below midline (7) 8–10 (11); peduncle scales (16–17) 18–22; predorsal scales 31–44 (45–49); interdorsal scales (9) 10–15 (16–17); prepelvic scales (20) 21–27 (28–30); anus-anal-fin scales 2–6; postdorsal scales (12) 13–20 (21–22); postanal scales (8) 9–14 (15); first dorsal (III) IV–VI; second dorsal I,8–11; pectoral 11–13 (14); pelvic 6; anal-fin I,(18) 19–25 (26); caudal (15–16) 17 (18) (Table 2).

Morphometrics: specimens examined 50.5–76 mm; short head, four times into SL; eye large, 2.5 times into maximum body depth. Body compressed and elongate, ratio of thoracic length to abdominal length less than 2, maximum body depth six to eight times in SL.

Premaxillary long, weakly protrusible, curving ventrally midway along length, creating muzzle-like snout; terminal mouth, with moderately long, posteriorly curved, pointed, conical teeth. Forked caudal fin; second dorsal and anal fins falcate; anal fin long, extending from anterior of first dorsal to posterior of second dorsal; pelvic fin extending to anus; first dorsal-fin origin opposite of anal-fin origin; pectoral fin pointed, extending to insertion of pelvic fin. First dorsal spinous, second dorsal with one anterior spine followed by branched rays. Genital papilla short in males, absent in females (Grier *et al.* 1990). Lateral line nearly absent, pored scales, if present, always found posterior to first dorsal usually concentrated on peduncle. Scales cycloid, extending onto caudal fin, absent from other fins; opercle scaled, scales extending to a spot below front of eye; top of head with or without scales, if present may extend to front of eye. Dorsal profile ascending gradually from tip of snout to supraoccipital, profile from supraoccipital to anterior insertion of second dorsal straight, and descending gradually to dorsal procurrent caudal-fin rays. Ventral profile forming gentle arc from snout to ventral procurrent caudal-fin rays.

Color in life. Body translucent, with yellow or green tint (Fig. 7). Breeding males with red muzzle and yellow to orange second dorsal, anal, and caudal fins. Midlateral silver band, narrowest on peduncle, broadening and fading anteriorly. Scales above midline and on dorsum outlined with melanophores, forming weak black stripe along center of dorsum. Venter with black stripe originating posterior to anus and terminating at the origin of the caudal fin. Distal one-third of first dorsal fin with melanophores on membranes forming a black band in males, not as pronounced in females. Head covered in melanophores, with supraoccipital densely pigmented, chin pigmented, dark spot on lower jaw at rear margin of mouth. Iris silver, dusky dorsally in some individuals, inside of mouth with scattered melanophores along margin and on outside of cheeks. Spines and rays outlined in melanophores, except on pelvic fin, which is devoid of pigment. Silver peritoneum visible through body wall.



FIGURE 7. Labidesthes vanhyningi live specimen. AUM 31984, 64.2 mm SL, Hillsborough River drainage, Hillsborough County, FL.

Color in alcohol: Body pallid, lateral silver stripe along the midline overlaying a dark stripe, fading and broadening anteriorly (Fig. 6). Scales above lateral stripe outlined in melanophores, dorsum with black stripe along middle. Venter with black stripe along middle, faint anterior to pelvic fin. Distal one-third of first dorsal fin with melanophores on membranes forming a black band in males, but not as pronounced in females. Head covered in melanophores, with occiput densely pigmented, lower jaw pigmented with dark spot at rear of mouth. Iris silver, dusky dorsally in some individuals, inside of mouth with scattered melanophores along margin and on outside of cheeks. Spines and rays outlined in melanophores, except in pelvic fin that is devoid of pigment.

Range. Labidesthes vanhyningi is known from Gulf of Mexico drainages from the Neches River (including the Lower Mississippi River) east around the southern tip of peninsular Florida and north to the Pee Dee River drainage (Fig. 1).

Etymology. Patronymic for O. C. Van Hyning, former Curator of Reptiles and Fishes of The Florida State Museum and collector of the holotype (Bean & Reid 1930).

Discussion

The only skeletal character useful in separating most *Labidesthes vanhyningi* from *L. sicculus* was the length of the anterolateral process of the post-temporal (< width of the base of the process in *L. vanhyningi* or > the width of the base of the process in *L. sicculus*). We were unable to verify this character in the type specimens, but it was observed in topotypes of both species. Three cleared and stained specimens under 57 mm SL, two from the Red River and one from the Detroit River, did exhibit the diagnostic skeletal character of *L. vanhyningi*. However, additional small specimens of *L. sicculus* under 60 mm SL were closer to the *L. vanhyningi* condition of the anterolateral process of the post-temporal, which suggests that the process forms as a sesamoid bone along the ligament later in life, and the character is useful in diagnosing specimens above 60 mm SL.

Meristics were taken on 315 specimens. The first five principal components in the principal components analysis (PCA) of meristics explained 89% of the variation observed in *Labidesthes* species, but when plotted against one another no separation was observed between *L. vanhyningi* and *L. sicculus*. The greatest degree of separation observed was the number of prepelvic scales, which were modally higher in *L. sicculus* than in *L. vanhyningi* (Fig. 8). This variation was not diagnostically significant because there was overlap in the number of prepelvic scales (22–32 scales in *L. sicculus* vs. 20–30 in *L. vanhyningi*) (Table 2).

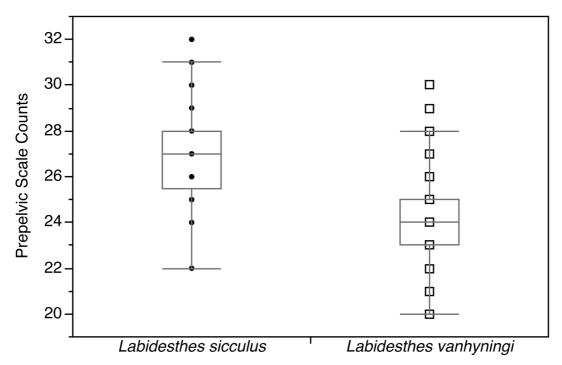


FIGURE 8. Box plots of prepelvic scale counts for *Labidesthes* species (p<0.00001).

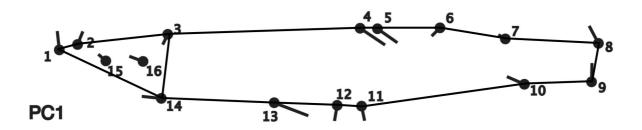


FIGURE 9. Geometric morphometric shape change vectors for Principal Component 1.

Principal components analysis of geometric morphometric data resulted in Principal Component 1 (PC1) explaining 29.39% of the variation and the first five components explaining a total of 73.5% of the observed variation. Principal Component 1 was most correlated with location of the pelvic fin along the venter (Fig. 9).

Bivariate plots among the first five Principal Components failed to show complete separation between species, but the two species were mostly separated along PC1 (Fig. 10).

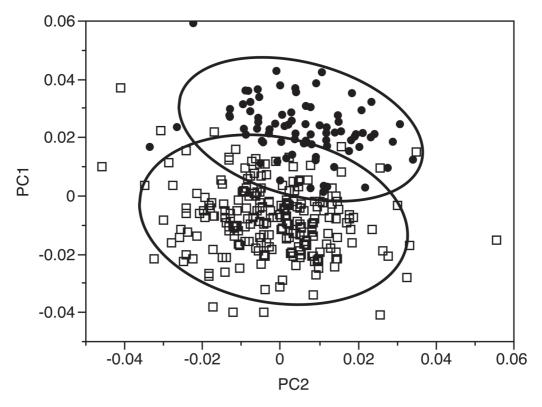


FIGURE 10. Results of geometric morphometric Principal Components Analysis of *Labidesthes sicculus* (circles) and *L. vanhyningi* (squares). PC 1 explained 29.386% of the variation and PC2 explained 18.366% of the variation.

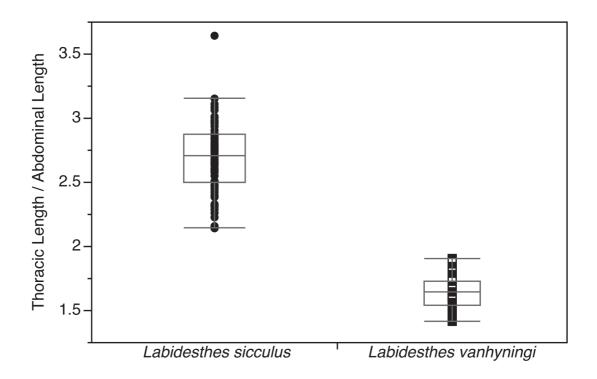


FIGURE 11. Box plots of abdominal/thoracic length in *Labidesthes* species (p<0.00001).

Pelvic-fin measurements were made on 64 *Labidesthes sicculus* and 58 *L. vanhyningi* specimens, including primary type material, after meristic and geometric morphometric data showed patterns indicating possible separation. Comparing thoracic length to abdominal length shows a complete and significant (p<0.0001) separation of the *Labidesthes* species (Fig. 11) indicating a more anterior pelvic fin in *L. vanhyningi* than in *L. sicculus*.

It is remarkable that *Labidesthes sicculus* and *L. vanhyningi* are both found in Gulf of Mexico drainages from the Sabine River to the Pascagoula River. In addition, *Labidesthes vanhyningi* was observed as far north in the Mississippi River drainage as Reelfoot Lake. While examining material to determine the range of *Labidesthes* species, eleven lots (NCSM 47153, UF 29501, TU 64284, TU, 76058, TU 110175, TU 121912, TU 122991, UT 158.88, UT 158.118, UT 158.292, UT 158.291) were found to contain both *L. sicculus* and *L. vanhyningi*, indicating that the two species were not only sympatric, but syntopic. The diagnostic characters of the species are clear cut, and the presence of both species sympatrically deserves further explanation.

The ecological conditions preferred by the two species appear to be different as is noted by figure 1. While *L. sicculus* ascends the western flank of the Applachians and US Interior Highlands, *L. vanhyningi* is confined to the lowlands, mostly below the Fall Line. The range of habitat preference of *L. sicculus* is wide, and the two come into contact along the Gulf Coast in areas up the Mississippi River. The species are maintaining their identities as we did not find any morphologically intermediate specimens. If their spawning modes are different, they would preclude the species interbreeding.

Labidesthes vanhyningi has recently expanded its range north of the Santee River into the Pee Dee and Cape Fear River drainages (Moser *et al.* 1998). Although historically well sampled, *L. vanhyningi* were not documented in the Pee Dee River basin but, based on museum records, seem to have become established in the Pee Dee since 1994. Presently, *L. vanhyningi* is only known from a single collection (NCSM 60434) of four individuals from the Cape Fear River basin, and may not represent a successful range expansion into the drainage.

Conclusion

Labidesthes vanhyningi and L. sicculus are separate species. Labidesthes species are diagnosable by the ratio of thoracic length to abdominal length in specimens over 55 mm SL (< 2 in L. vanhyningi vs. >2 in L. sicculus), the shape of the midlateral stripe (not tapering anterior of first dorsal in L. vanhyningi vs. tapering anterior of first dorsal in L. sicculus, and the length of the anterolateral process of the post-temporal in specimens over 60 mm SL (< width of base in L. vanhyningi vs. > width of base in L. sicculus).

Acknowledgements

This manuscript represents part of a MS thesis from Auburn University. We would like to thank M. Retzer (INHS), W. Starnes and G. Hogue (NCSM), H. Bart and N. Rios (TU), D. Nelson and A. Barget (UMMZ), R. Mayden and B. Kuhajda (UAIC), L. Page and R. Robins (UF), J. Williams and S. Raredon (USNM), J. Parris Joice (UT), M. Warren with the USDA Forest Service Southern Research Station for access to and loans of specimens. Thanks to C. Allison, J. Evans, S. Herrington, C. Johnston, T. Pera, and many others for help collecting specimens. Thanks to S. Ferdous and C. Stout for feedback on this manuscript. This paper is contribution No. 709 of the Auburn University Musuem of Natural History.

References

Adams, D.C., Rohlf, F.J. & Slice, D.E. (2004) Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology*, 71, 5–16.

http://dx.doi.org/10.1080/11250000409356545

Bailey, R.M., Winn, H.E. & Smith, C.L. (1954) Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 106, 109–164.

Barbour, C.D. (1973) The systematics and evolution of the genus *Chirostoma* Swainson (Pisces: Atherinidae). *Tulane Studies in Zoology and Botany*, 18 (3), 97–141.

- Bean, B.A. & Reid, E.D. (1930) On a new species of brook silverside, *Labidesthes vanhyningi*, from Florida. *Proceedings of the Biological Society of Washington*, 43, 193–194.
- Bloom, D.D., Piller, K.R., Lyons, J., Mercado-Silva, N. & Medina-Nava, M. (2009) Systematics and biogeography of the silverside tribe Menidiini (Teleostomi: Atherinopsidae) based on the mitochondrial ND2 gene. *Copeia*, 2009, 408–417. http://dx.doi.org/10.1643/CI-07-151
- Boulesteix, A.-L. (2005) A note on between-group PCA. *International Journal of Pure and Applied Mathematics*, 19, 359–366.
- Cahn, A.R. (1927) An ecological study of southern Wisconsin fishes; the brook silverside (*Labidesthes sicculus*) and the cisco (*Leucichthys artedi*) in their relations to the region. *Illinois Biological Monographs*, 11, 1–151. http://dx.doi.org/10.5962/bhl.title.50172
- Chernoff, B. (1986) Phylogenetic relationships and reclassification of Menidiinae silverside fishes with emphasis on the tribe Membradini. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 138, 189–249.
- Cope, E.D. (1865) Partial catalogue of the cold-blooded vertebrata of Michigan. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 17, 78–88.
- Cope, E.D. (1870) A partial synopsis of the fishes of the fresh waters of North Carolina. *Proceedings of the American Philosophical Society*, 11, 448–495.
- Dyer, B.S. & Chernoff, B. (1996) Phylogenetic relationships among atheriniform fishes (Teleostei: Atherinomorpha). *Zoological Journal of the Linnean Society*, 117, 1–69. http://dx.doi.org/10.1111/j.1096-3642.1996.tb02148.x
- Etnier, D.A., & W.C. Starnes (1993) Atheriniformes: Family Atherinidae—The Silversides. *In: The Fishes of Tennessee*. The University of Tennessee Press, Knoxville, 681 pp.
- Grier, H.J., Moody, D.P. & Cowell, B.C. (1990) Internal fertilization and sperm morphology in the brook silverside, *Labidesthes sicculus* (Cope). *Copeia*, 1990, 221–226. http://dx.doi.org/10.2307/1445838
- Hubbs, C.L. (1921) An ecological study of the life-history of the fresh-water atherine fish *Labidesthes sicculus*. *Ecology*, 2, 262–276.
 - http://dx.doi.org/10.2307/1928980
- Hubbs, C.L. & Allen, E.R. (1943) Fishes of Silver Springs, Florida. *Proceedings of the Florida Academy of Sciences*, 6, 110–130.
- Hubbs, C.L. & Lagler, K.F. (1947) Fishes of the Great Lakes Region. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 213 pp.
- Klingenberg, C.P. (2011) MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology and Natrual Resources*, 11, 353–357.
 - http://dx.doi.org/10.1111/j.1755-0998.2010.02924.x
- Klingenberg, C.P. & Monteiro, L.R. (2005) Distances and directions in multidimensional shape spaces: implications for morphometric applications. *Systematic Biology*, 54, 678–688.
- http://dx.doi.org/10.1080/10635150590947258
- Klingenberg, C.P. & Spence, J.R. (1993) Heterochrony and allometry: lessons from the water strider genus *Limnoporus*. *Evolution*, 47, 1834–1853.
 - http://dx.doi.org/10.2307/2410225
- Lee, D.S. (1978) *Labidesthes sicculus* (Cope), Brook silverside. *In: Atlas of North American Freshwater Fishes.* N. C. State Museum of Natural History, Raleigh, pp. 557.
- Marsden, J.E., Langdon, R.W. & Good, S.P. (2000) First Occurrence of the Brook Silverside (*Labidesthes sicculus*) in Lake Champlain, Vermont. *Northeastern Naturalist*, 7, 248–254. http://dx.doi.org/10.1656/1092-6194(2000)007[0248:FOOTBS]2.0.CO;2
- Mayr, E. (1942) *Systematics and the origin of species, from the viewpoint of a zoologist*. Colombia University Press, New York, 334 pp.
- Mitteroecker, P. & Bookstein, F.L. (2011) Linear discrimination, ordination, and the visualization of selection gradients in modern morphometrics. *Evolutionary Biology*, 38, 100–114. http://dx.doi.org/10.1007/s11692-011-9109-8
- Moser, M.L., Rohde, F.C., Arndt, R.G. & Ashley, K.W. (1998) Occurrence of the brook silverside, *Labidesthes sicculus* (Atheriniformes:Atherinidae), in North Carolina. *Brimleyana*, 25, 135–139.
- Page, L.M. & Burr, B.M. (2011) *Peterson Field Guide to Freshwater Fishes of North America North of Mexico*. Houghton Mifflin Harcourt, New York, 663 pp.
- Powles, P.M. & Sandeman, I.M. (2007) Growth, summer cohort output, and observations on the reproduction of brook silverside, *Labidesthes sicculus* (Cope) in the Kawartha Lakes, Ontario. *Environmental Biology of Fishes*, 82, 421–431. http://dx.doi.org/10.1007/s10641-007-9304-8
- Rasmussen, R.P. (1980) Egg and larva development of brook silversides from the Peace River, Florida. *Transactions of the American Fisheries Society*, 109, 407–416.
 - http://dx.doi.org/10.1577/1548-8659(1980)109%3C407:EALDOB%3E2.0.CO;2
- Rohlf, F.J. (2013) *tpsDig2 version 2.17*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

- Rohlf, F.J. (2013) *tpsUtil version 1.58*. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.
- Rohlf, F.J., Loy, A. & Corti, M. (1996) Morphometric analysis of Old World Talpidae (Mammalia, Insectivora) unsing partial-warp scores. *Systematic Biology*, 45, 344–362.
 - http://dx.doi.org/10.1093/sysbio/45.3.344
- Rohlf, F.J. & Marcus, L.F. (1993) A revolution in morphometrics. *Trends in Ecology and Evolution*, 8, 129–132. http://dx.doi.org/10.1016/0169-5347(93)90024-J
- Rohlf, F.J. & Slice, D.E. (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology*, 39, 40–59.
 - http://dx.doi.org/10.2307/2992207
- Rowe, J.W. (1992) The sturgeon chub and the brook silverside in the Platte River of Nebraska. *Prairie Naturalist*, 24, 281–282. Sabaj Pérez, M.H. (Ed.) (2014) Standard symbolic codes for the institutional resource collections in herpetology and ichthyology: an Online Reference. Version 5.0 (22 September 2014). American Society of Ichthyologists and Herpetologists, Washington, DC. Accessible from: http://www.asih.org/resources/standard-symbolic-codes-institutional-resource-collections-herpetology-ichthyology/ (accessed 05 January 2015)
- Scharpf, C. & Lazara, K.J. (2014) The ETYFish Project. 27 August 2014—Cope headscratcher #6: *Labidesthes sicculus*. Available from: http://www.etyfish.org/names-of-the-week2014/ (accessed 05 January 2015)
- Taylor, W.R. & van Dyke, G.C. (1985) Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9, 107–119.